

## IMPACT OF THE HUMAN EGALITARIAN SYNDROME ON DARWINIAN SELECTION MECHANICS

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*Abstract.*—With nothing more than kin selection and reciprocal altruism theories to work with, the selection basis of human degrees of altruism and cooperation is often difficult to explain. However, during our prehistoric foraging phase, a highly stable egalitarian syndrome arose that had profound effects on Darwinian selection mechanics. The band's insistence on egalitarianism seriously damped male status rivalry and thereby reduced the intensity of selection within the group by reducing phenotypic variation at that level, while powerful social pressure to make decisions consensual at the band level had a similar effect. Consensual decisions also had another effect: they increased variation between groups because entire bands enacted their subsistence strategies collectively and the strategies varied between bands. By reducing the intensity of individual selection and boosting group effects, these behaviors provided a unique opportunity for altruistic genes to be established and maintained. In addition, the egalitarian custom of socially isolating or actively punishing lazy or cheating noncooperators reduced the free-rider problem. In combination, these phenotypic effects facilitated selection of altruistic genes in spite of some limited free riding. This selection scenario remained in place for thousands of generations, and the result was a shift in the balance of power between individual and group selection in favor of group effects. This new balance today is reflected in an ambivalent human nature that exhibits substantial altruism in addition to selfishness and nepotism.

In spite of many brilliant attempts to explain instances of altruistic behavior (see, e.g., Trivers 1971, 1972; Alexander 1974, 1987; E. O. Wilson 1975; Alexander and Borgia 1978), a selection paradox continues to confront us wherever unreciprocated acts of reproductive generosity toward nonkin take place. Although in many instances such donations can be explained convincingly in terms of kin selection, not infrequently our current main theories (inclusive fitness and theories of reciprocity) seem to be stretched beyond their limits. This is particularly the case when it comes to human degrees of altruism and cooperation. Were group selection able to operate robustly, this could explain such behavior. However, to make this possible mechanically, some radical shifts in variation or in extinction rates would be needed (see Williams 1966). It is well established that typical extinction rates and levels of variation in mammalian social species are not automatically conducive to group selection, as they are for the social insects (see Seeley 1997).

A theory of group selection is presented here that will be applied initially only to humans. I shall address a neglected interaction between a distinctively human cultural syndrome and Darwinian selection mechanics, an interaction that involves sharp modification of variation between and within groups. Because culture is involved, the variation I discuss here is exhibited at the level of pheno-

type rather than at the level of genotype. The hypothesis is quite specific: the well-documented equality-based social traditions of human foragers drastically modify the balance of power between within-group selection and between-group selection. These cultural traditions have an effect such that individual effects are vitiated at the same time that group effects are being amplified, so this hypothesis provides the basis for a logical and parsimonious explanation of those altruistic acts that extend helping behavior beyond offspring and close kin to all members of the group. It also provides some major assistance in explaining the cooperation that is so evident among the human foragers in whose groups our own genes evolved.

The hypothesis, then, is that a far-reaching political invention, namely, hunter-gatherer egalitarianism as defined by anthropologists (see Fried 1967; Service 1975; Boehm 1982*a*, 1982*b*, 1993, 1997; Knauff 1991, 1994*b*), had profound and fundamental effects on Darwinian selection mechanics. Obviously, for a distinctive cultural way of doing things to affect selection mechanics in a way that could influence the long-term selection of behavioral traits at the level of genes, the cultural tradition in question would have to be in place for thousands of generations. This condition is met, for our prehistoric human predecessors remained consistently egalitarian for scores, probably hundreds, of millennia (see Mithen 1990; Knauff 1991; Boehm 1997).

In this evolutionary context, I discuss three separate effects of what I call the egalitarian behavioral syndrome: it damped phenotypic variation within groups, it amplified phenotypic variation between groups, and it enabled a moralistically watchful species to control the antisocial behaviors of individuals who carried genes for free riding. These three cultural effects substantially empowered the genetic selection of traits making for altruism and cooperation.

The egalitarian syndrome required the invention of the human moral community (Boehm 1997), and it seems likely that both were in place 100,000 yr ago—and probably earlier—among anatomically modern humans. I make this assertion because both are universal among extant human foragers who remain highly nomadic. The syndrome in question involves moralistic suppression of status rivalry, morally enforced consensual decision making, and policing of free riders. I shall discuss this syndrome in some detail because each of these three patterns acted in its own way to assist the selection of altruistic traits. Because of limitations of scope, I shall not try to discuss how the genetic potential for egalitarianism itself was established, nor shall I discuss in general the selection of altruistic behaviors through proximate mechanisms that are cultural (Campbell 1972; see also Boyd and Richerson 1985). The focus is on the direct effects of these egalitarian behaviors on phenotypic variation both within and between groups and the impact on basic Darwinian selection mechanics as this affected the selection of altruistic traits at the level of genes.

Some further definition is in order. The altruistic traits to be discussed may be defined conventionally as behaviors that transfer reproductive resources from donors to other individuals who are genetic competitors. However, when I focus on reproductive generosity that depends on either kin selection (Hamilton 1964) or parental investment (Trivers 1972), I shall refer to “kin altruism.” When in-

dividual reproductive generosity accrues to all group members equally or to unrelated individuals in the same group, I shall refer to this as "generic altruism." Kin altruism is readily explained by inclusive fitness models and poses no selection paradox so long as inclusive benefits outweigh individual costs. The arguments made here will help resolve the selection paradox posed by generic altruism in humans. Whether these arguments apply to other highly social species will depend on the degree to which their behaviors suppress within-group variation, amplify between-group variation, or curtail free riding.

Two other possibilities might also assist selection of generically altruistic traits. One is an augmentation of extinction rates at the group level; the other is what might be called pleiotropic effects. With extinction rates the argument is straightforward: if group extinction rates are raised, as by intensive warfare, group selection is empowered (see Alexander 1974). Pleiotropic arguments are a bit more complicated. The assumption is that certain traits that are powerfully selected through inclusive fitness, such as maternal protection of offspring, could be extended occasionally to nonkin if natural selection were mechanically unable to segregate the two behaviors and eliminate the latter. In effect, the first behavior with its very sizable reproductive rewards would be subsidizing the second (for examples, see Boehm 1981; Simon 1990; see also Eibl-Eibesfeldt 1996). These two possibilities are not discussed here.

#### ALTRUISTIC TRAITS AND THEIR EXPLANATION

This article is mainly about the effect of phenotype on levels of selection. For three decades, the received wisdom has been that group effects are simply too weak to matter very much for humans. However, even after Williams's (1966) well-founded attack, group selection theory has attracted significant critical exploration (e.g., Durham 1976, 1991; Alexander and Borgia 1978; Wade 1978; Wilson 1978; Campbell 1983, 1994, Boyd and Richerson 1985, 1991; Alexander 1987; Frank 1988; Hamilton 1991; Campbell and Gatewood 1994) and even a handful of proponents, particularly in biology (e.g., D. S. Wilson 1975, 1977, 1980, 1983, 1989, 1990, in press, unpublished manuscript; Wade 1978; Boyd and Richerson 1985, 1991, 1990; Wilson and Sober 1994) but also anthropology (e.g., Boehm 1976, 1978, 1981, 1982*a*, 1982*b*, 1996, 1997; Goldschmidt 1976; Knauff 1989, 1991, 1994*a*, 1994*b*; Soltis et al. 1995; S. Lansing and B. Smuts, unpublished manuscript) and ethology and primatology (e.g., Eibl-Eibesfeldt 1982, 1989; Vehrencamp 1983; van Hoof and van Schaik 1992; Strier 1994).

In building on this work, I develop here a biocultural model for humans, one that demonstrates that Darwinian selection mechanics were, in the late Paleolithic, substantially altered in favor of selection at the group level. In considering this argument, one must keep in mind that this important phase of human evolution took place with people living basically in smallish bands averaging perhaps 30 persons (Dunbar 1996), bands that, though flexible in composition (see Palmer et al., in press), had some substantial continuity over time and usually made short-term foraging decisions as units, including emergency decisions that

were immediately critical to reproductive success (see Boehm 1996). Thus, the structural requirements for group selection definitely were present in terms of selection on a short-term basis (see Wilson and Sober 1994).

Although responses to Wilson and Sober's (1994) review of multilevel selection theory were mixed, a number of biologists and others seem to agree that on a logical basis, group effects have too often been ignored or underestimated. In that forum, Campbell and Gatewood (1994) emphasized, for humans, that although multilevel selection theory fulfills logical needs of scientific explanation, it remains to posit specific and convincing mechanisms, mechanisms that would enable group effects to be strong enough to hold their own when competing with the acknowledged power of individual (inclusive) effects. "What we need are detailed plausible scenarios as to how biological group selection took place under the conditions of early human evolution. . . . We also need speculation on the more specific group-selected innate traits involved" (p. 614). Here I shall develop on a preliminary basis precisely the analysis that Campbell and Gatewood call for.

### THREE CULTURAL FACTORS THAT EMPOWER GROUP SELECTION

In evolutionary biology it is agreed that whenever within-group selection and between-group selection are working against each other, as with any generically altruistic trait, selection at the individual level should be winning hands down because of its higher rate of evolution. This rate is driven by the much higher extinction rates that prevail for individuals as gene-carrying vehicles of selection (E. O. Wilson 1975; Alexander and Borgia 1978; see also Wilson and Sober 1994) and also by the fact that genotypic variation tends to be higher within than between groups because of averaging tendencies. My argument will be that we can set aside variation at the level of genotype and concentrate on variation at the level of phenotype, precisely because natural selection operates on phenotype, not genotype. I shall use a multilevel selection model for prehistoric humans to suggest that consistent and powerful cultural influences impacted individual and group rates of phenotypic variation in very different directions and thereby substantially realigned the balance of power between group and individual selection.

As we engage with three relevant aspects of the egalitarian syndrome (suppression of competition, consensual decisions, and effective policing of free riders), some important ethnographic assumptions must be made. One is that even though there existed in the late Paleolithic a rather wide variety of types of highly nomadic hunter-gatherers, living in varied natural and political environments (Kelly 1995), they all lived in bands that were politically egalitarian, and they all made strategically important decisions by seeking a consensus (see Mithen 1990; Knauft 1991, 1994*b*; Boehm 1993, 1994*b*; Erdal and Whiten 1994, in press; Kelly 1995). Such foragers made very significant contributions to the evolution of modern human gene pools (Tiger and Fox 1966); indeed, they are directly responsible for any unusual capacities that modern humans may have for generically altruistic and cooperative behavior.

*Egalitarianism Suppresses Individual Competition*

Egalitarianism does not just happen; it is *made* to happen (Lee 1979; Boehm 1982a, 1993; Woodburn 1982). All nomadic foragers are egalitarian, a pattern that makes the adult males, and sometimes also the females, into equals as household heads. They are politically egalitarian to the degree that named leadership roles are lacking or devoid of authority, status differences among politically autonomous household heads are muted, and individuals who try to influence group decisions must do so very circumspectly. The guidance mechanism for this deliberate behavior is an egalitarian ethos (Cashdan 1980) that involves a set of indigenous attitudes that make for strong valuation of personal autonomy of adults (Gardner 1991). These values help generate group hostility toward any individual who even attempts to assume a serious role of authority in the band, let alone baldly tries to coerce other adults. Alpha-male types are not allowed to flourish, even though the tendency to engage in status rivalry and seek dominance persists and can still be expressed within carefully circumscribed limits (see Fried 1967).

In effect, there is a vigilant sharing of power by an entire band (Boehm 1994b) that makes its decisions by consensus, just as there is vigilant sharing of large-game meat (Erdal and Whiten 1994). Political bullies and overly aggressive or highly successful individuals, who might wish to monopolize resources such as meat or women, are subject to sanctions that include not only gossip but direct criticism, ridicule, ostracism, exile, and execution (Boehm 1993). This means that reproductive advantages associated with high rank in other hierarchical species (see Ellis 1995) are reduced. Underlying this suppression of competition and domination are counterdominant attitudes (Erdal and Whiten 1994) that spring from a natural aversion to being subordinated (Boehm 1984, 1997; Knauff 1994b), and in effect they turn the usual primate dominance pyramid upside down: the group, acting decisively as a subordinate coalition, decisively dominates its alpha-male types instead of vice versa (Boehm 1993; but see also Boehm 1994b, 1997; Erdal and Whiten 1994, 1996; Knauff 1994b).

Most self-aggrandizing or dominant behavior is nipped in the bud, but occasionally a shaman, who uses power selfishly rather than altruistically as is socially expected, may intimidate group members to the degree that he becomes a despot. He then begins to monopolize food or women (Balikci 1970). If magical antidotes do not seem to be working, eventually there will be a conspiracy to eliminate him by means of physical execution (Boehm 1993). Less feared would-be dominators can be coped with through ostracism or exile, which also impose reproductive costs. Very often, ambitious or aggressive individuals (including group leaders) decide not to take such risks, even though their deviant domineering propensities may be apparent to everyone (e.g., Briggs 1970). In effect, the group intimidates its stronger, more gifted, or more assertive members to keep them in line, but at the same time it uses them, in strictly limited ways, for purposes of leadership or meat procurement.

Everywhere nomadic foragers arrive at very similar general covenants about how people should behave: they favor political autonomy, sharing, cooperation, and being helpful to others (Knauff 1991). We also know that morality always

has to work against certain aspects of human nature that make for selfishness, nepotism, and aggressiveness (see Campbell 1972, 1975). On this basis, the degree of sharing and cooperation we see in forager groups results not only from innate tendencies but from awareness of rewards that cooperation can bring and from fear of censure or worse if one behaves deviantly. Certain forms of nonaltruism, such as trying to control other household heads or failing to share meat, are deemed to be very seriously deviant.

What the group sees to is that no individual (or family) dominates any other by interfering with their autonomy and that certain scarce and divisible resources are spread rather evenly among the group's households. This conscious concern applies most directly to large-game meat and political power, but it is worth noting that the nearly equalized sharing of large-game meat also helps damp tendencies toward polygamous marriage that favor the best hunters (e.g., Balikci 1970). The immediate result is that phenotypic differences among genetic competitors within the same group are leveled quite drastically, independently of their genotypic differences.

When foragers suppress differences among individuals, they understand exactly what they are doing in terms of evening out disparities in authority, status, or material resources, and such leveling has profound effects on the expression of social hierarchy. This is true not only with simpler foragers as defined by Woodburn (1982) and Knauff (1991) but also with complex foragers (Price and Brown 1985) and a wide variety of postdomestication populations living in small tribal communities (Service 1975) and also certain modern utopian groups (Wilson and Sober 1994). All may be considered intentional communities that are ideologically committed to substantial equalization of power and material benefits (Boehm 1993). This human capacity to create a societal blueprint and then enact it is one thing that makes us rather different from other species.

When people first began to level their own hierarchies to the degree that extant foragers do, this made individuals with their immediate families—previously the key vehicles of natural selection for humans—far less subject to phenotypic variation. The result was a significant reduction in the power of selection effects within the group, which of course made it more difficult for within-group effects to swamp group effects and thereby suppress the gene frequencies for altruistic traits. This realignment of selection forces is significant for thinking about the group selection quandary more generally, for with altruism the problem is always the weakness of between-group effects in relation to the strength of within-group effects. If we compare egalitarian foragers with the hierarchical African great apes—or with humans who live in decidedly nonegalitarian chiefdoms or modern nations—there can be no doubt that the moralistic, antihierarchical leveling behavior of prehistoric hunter-gatherers seriously modified the balance of power between these two levels of selection in favor of group selection (Boehm 1997).

#### *Consensus Seeking at the Band Level*

Our second cultural factor involves a group-based behavior that not only further reduces the power of individual selection but amplifies the power of selection at the group level on an absolute basis. These two functions will be dis-

cussed separately. When foragers identify an ecological, political, or social problem that threatens or concerns the entire group, they do their best to cope with it as a group. They believe in reaching unanimity for good reason, for as nomads they must either agree on a single foraging strategy or else split into family groups, and they fully understand the benefits of cooperating as a larger group. The way they manage to stay together as a band is very interesting.

*Leveling of individual differences.*—To keep the band intact, hunter-gatherers place considerable social pressure on dissenters when migration decisions are being made (e.g., Lee 1976); this is a normal part of consensus seeking (see Mithen 1990; Knauft 1991). If they manage to hammer out a consensus, and they usually do, there are a number of advantages. They can continue to pool their knowledge about the environment, and they can continue subsistence activities that depend on a relatively large number of people working together, as with cooperative hunting or sharing of large game. They also have fellow band members to assist them in emergencies; in any event, foragers love society. If there is any friction between bands over resources or past homicides, then staying in a larger group also may bring security advantages in the political-territorial sphere.

This collective bias in arriving at decisions that involve group welfare is universal among foragers (see Knauft 1991); with the absence of strong leaders, consensus seeking is how they go about coping decisively—as a group—with problems that affect everyone in the group. Band members benefit not only because they can cooperate in larger numbers but because group strategies are informed by pooled knowledge and experience (Mithen 1990). Consensus seeking keeps individuals who might make inferior (or superior) decisions on their own from doing so, and it thereby reduces phenotypic variation among individuals and family groups within the band. Thus, seeking a consensus at the band level acts to weaken the force of selection by inclusive fitness and thereby shifts the selection balance of power still further in favor of group effects.

*Intensification of intergroup variation.*—This next phase of the argument is particularly important. So far, I have accounted for substantial diminishment of selection effects that take place within groups but for no absolute empowerment of the relatively very weak selection effects that take place between groups. We now must consider the effects on natural selection mechanics when consensus seeking at the band level leads to amplification of phenotypic differences between groups.

Sharing of fitness at the group level can be obligate (Miller 1994), as when prehistoric human foragers faced pack-hunting predators or, possibly, genocidal warfare. Sometimes, however, the collective sharing of fitness becomes voluntary; this takes place whenever an entire band insists on consensuality and then enacts its decision uniformly. Because of the recurrent challenge of where to migrate next, foragers do this quite regularly (see Hill et al. 1987; Cashdan 1990; Mithen 1990). Particularly during off years, such decisions can be quite critical to reproductive success (see Kelly 1995; Boehm 1996), and vagaries of the human imagination—and of specific environmental information developed by different groups—can make such decisions significantly variable between groups (see also Boehm 1978).

Decades ago, anthropologists began to realize that nonliterate humans pool their knowledge and cope with environmental problems on a collective and anticipatory basis (see Goldschmidt 1959, 1976; Bennett 1976; Boehm 1976, 1978), yet group problem solving among nonliterates has not been descriptively well represented in ethnographic publications. In emphasizing the evolutionary importance of the few anecdotal accounts available, in passing I suggested (Boehm 1978, pp. 282–283) that prehistorically group selection effects were being amplified whenever genetically competing groups made decisions of varying wisdom as they coped with ecological problems (see also Campbell 1983). More recently, I have analyzed some exemplary tribal case histories and have applied this further analysis to prehistoric foragers who made decisions as bands (Boehm 1996; see also Mithen 1990; Wilson and Sober 1994). In both instances, the argument was that varying consensual decisions intensify phenotypic variation rates at the level of bands or nexuses of bands.

Thus, whenever reproductively relevant decisions vary between entire groups that are in a position to replace one another, this should and will result in group selection because natural selection operates on phenotype. As a practical matter, group unanimity is not always forthcoming; if band members fail to agree on the same foraging strategy or if they agree that resources are temporarily too dispersed, the group may split up for a time into separate households. When individual families split off, the individual level of selection becomes empowered to the degree that different households follow different adaptive strategies and suffer different fates with respect to the inclusive fitness of their members. However, when the heavily favored communal approach succeeds, then selection at the band level can be empowered significantly and on an absolute basis.

In developing a few scenarios to support this very consequential interpretation, I shall be emphasizing emergency decisions because these involve critical problems with key natural resources, and such crises greatly intensify the rate of natural selection in general (see Odum 1993). With respect to variation among local decision units like bands, we know for nonliterate egalitarian groups more generally that their successes in the face of reproductively threatening problems can be spectacular (Boehm 1996) but also that these same groups are capable of falling into very serious strategic errors (Edgerton 1992). It is this possibility of brilliant successes and calamitous mistakes that so strongly amplifies the power of group selection, particularly when emergencies arise.

Many of the problems that foragers can cope with realistically emanate from the natural environment (drought, other meteorological perturbations, invasions by insects, certain health problems where etiology is understood, major shifts in migration patterns of large-game animals). Others emanate from the external political environment (territorial competition, revenge expeditions, raiding between groups) or the internal social environment (as in dealing with dangerous or disruptive problems of willful deviance or insanity). Whenever such problems are dealt with collectively, positive or negative reproductive consequences will impact at the group level. As a result of this sharing of fitness consequences in the face of dire threats, there are surely some extinctions and near-extinctions of bands. But probably more important over the evolutionary long haul is the less



dramatic demographic growth or decimation of such groups, which stems from a combination of emergency and routine decision making.

Information about emergency coping is scarce for extant foragers whose situations are relatively pristine, but, with some ancillary help from other nonliterate, including a few acculturated foragers (see Laughlin and Brady 1978), I have built some conservative hypotheses for foraging bands in general (Boehm 1996). For example, one band deals with a famine by seeing to it that everyone gets enough food to survive, whereas its neighbor stays together as a band (because of water supply) but stops sharing food entirely. Such behavioral disparities can have differential reproductive consequences at the group level. I emphasize, however, that neither strategy is necessarily a right one. In a relatively brief but severe drought that affects a large region, all members of the first band may barely survive the famine because they cooperated, whereas in the second band only a handful of unusually productive (or lucky, or selfish) households may survive even though they survive it rather well. In terms of group selection, the first band gains a major demographic edge. However, during a really protracted drought, the entire first band may starve to death, while a talented (or lucky) household or two of the second band might barely survive to breed again. In this instance, the second band wins the genetic race.

Bands as vehicles for group selection may experience short-term phenotypic variation with immediate fitness consequences in many other ways. In a given environmental emergency, one band may arrive at a realistic coping strategy and begin to implement it actively, while another band simply gives up, stays in place, and trusts to luck. In desperation a third band may rely solely on manipulations that they feel to be active but that are supernaturally based and have no realistic effect in solving the problem, aside from preventing migration or dispersion and creating optimism. A fourth may migrate permanently as a unit to another home range, while a fifth may decide to disband and try to join various other bands. Such varying collective decisions, along with passive failures to do anything at all, are fraught with reproductive consequences.

Of course, if members of a band cope with an emergency by merely making decisions as households, as in the fifth instance, then households become the significant vehicles of selection and inclusive fitness gets a boost as they go their own ways. However, a multilevel approach is still needed to calculate the overall reproductive effects, for that band will tend to reassemble when the emergency is over and will continue its genetic competition with neighboring bands that have followed a different, more nearly collective course.

Although varying band decisions surely amplify group selection for humans, one must consider cultural diffusion as a potential counterforce. In spite of the fact that we often behave as archtraditionalists (see Campbell 1975) and are ethnocentrically critical of other people's customs (LeVine and Campbell 1972), we also appear to be natural copycats (Boyd and Richerson 1985). Interband diffusion effects will tend to make the more basic patterns of decision making converge, particularly if bands are adjacent with frequent and friendly exchange of personnel; but even so, differences of information, individual intelligence or personality, and group dynamics will make for intergroup variation at the same

time. Thus, varying localized information in combination with individual variance among individuals who influence decisions may lead to varying group strategies; however, two nearby bands may also put exactly the same information to different uses.

Coping with emergencies may augment such phenotypic variation. If an environmental problem is exceptionally sudden, unusual, and severe, then there may not be time for interband exchange of specific information or discussion of strategic alternatives. Furthermore, many forager bands have hostile relations with at least some of their neighbors (see Kelly 1995; Keeley 1996); when groups engage in raiding aimed at killing opponents or stealing their women, the groups concerned are hardly going to share information about their strategies. In short, as an enemy of interdemic variation, the copycat problem is far from terminal. Bands that are close enough to replace each other as indirect (or direct) genetic competitors are free to vary their strategies in an independent fashion and do so.

There are, however, some serious problems with the identification of bands as long-term selection vehicles if one has in mind a neatly delineated vehicle that has fixed boundaries over time. It is well known that bands tend to be rather dynamic in composition, in that often marriages are band exogamous and a given couple can take up alternating residence with two sets of in-laws or other relatives. Thus, even though both foragers and anthropologists agree that bands exist as a type of group, over time the average band is far from being a closed or permanent entity (Palmer et al., in press). One might ask whether genetic group selection could operate on such units, but Wilson and Sober (1994) have made the important point that group selection does not require permanent groups with nonporous boundaries to operate. If a momentarily stable group shares the same fate during a brief but reproductively significant selection event, group effects result no matter what its members do afterward. My emphasis on emergency decisions (Boehm 1996) fits with that type of group selection.

Obviously, a group selection argument is furthered if groups tend to experience some continuity, and in this light foragers must be considered in all of their segmental manifestations, not just as people who always live in bands. Among Kalahari foragers, the minimal stable group-level vehicle for longer-term group selection of altruistic traits would be the core of families, usually not closely related, that are most closely associated with a proprietary resource such as a water hole (e.g., Lee 1979); with other foragers, this may apply to hunting and gathering ranges (Kelly 1995). The more that such multifamily cores stay together over time, the more consistent and powerful longer-term group selection effects are likely to be. As a somewhat larger vehicle of group selection, one also must consider the small cluster of bands, or nexus (see Heintz 1972), whose members intermarry and visit a great deal and stay separate socially from other nexuses. Where social boundaries as opposed to perimeter defense are used to keep others from exploiting local resources, such nexuses are predictable (see Kelly 1995) and likely to be rather stable: the moving of families from band to band is far more likely to take place within the nexus than without, and coping patterns are more likely to be shared within the nexus than without. In a sense,

a nexus can be considered as a kind of “superband,” a larger vehicle for selection at the group level that also can experience some internal group selection effects to the degree that its constituent bands may sometimes arrive at differing adaptive strategies.

Thus, over the longer term the patterns of ecological coping can be expected to vary not only between adjacent or nearby band cores but also between adjacent nexuses that tend to be culturally isolated because of ethnocentric hostility. In the short run, however, in the absence of nexuses a single band does actually behave as a well-bounded unit when immediate emergencies are faced—it does so just so long as a consensus is reached and executed. Whenever band members take uniform action, and thereby share the same immediate fate, the band serves as a very tidy short-term vehicle of group selection (see Boehm 1996).

Moderate ecological emergencies arise frequently, ones that cause bands to adjust their strategies, and drought is not the only problem; for example, the Mongongo nuts on which certain Kalahari foragers depend quite heavily can be affected by too much rain, which can either damage the blossoms or (later) cause the nuts to rot on the ground (Lee 1984). The resulting strategy adjustments may vary among bands, and there may be differential reproductive consequences. If hunter-gatherers in a region are facing a dire emergency, such as consequences of too much rain followed by a drought, then their collective failures and collective successes can have a very sharp impact on the intensity of group selection because possibilities for behavior-based demographic changes are amplified.

This means that in a variety of time frames a variety of group types—multi-family band cores, entire bands, and nexuses of bands where such exist—are all likely vehicles of group selection because they can vary significantly in the reproductively significant decisions they make. I should add that although I have focused mainly on reactions to dire and immediate ecological threats, longer-term, routinized collective decision-making patterns about migration strategy are also relevant because they may contribute to differences among units. Furthermore, it is not just foraging decisions that create variation. There are decisions about how to deal with dangerous deviants such as psychotic recidivist killers in the band and decisions made in dealing with competing groups. Here, just as with migration decisions, there can be marked differences of strategy—and of effectiveness in executing strategies—from one band to another. The result is an amplification of phenotypic variation between groups and therefore a mechanical empowerment of group selection effects.

Such empowerment takes place because groups with varying strategies will experience differential rates of growth or decline, and some with bad luck or very poor judgment may experience extinction. Outright extinctions seem particularly likely where groups compete directly, but opinions have varied greatly with respect to genocidal warfare in prehistoric times (see Alexander 1974; Moore 1994; Keeley 1996 for open-minded views). If we go by patterns that appear sporadically among today’s foragers (see Kelly 1995), there could have been rather frequent raiding for females, active conflicts over use of critical resources like water, revenge expeditions after intergroup homicides took place,

and also retaliatory patterns based on the assumption that deaths of band members can be caused by sorcery from other bands. While total genocide perpetrated by one group on another through a single attack may be questionable for foragers as a frequent or widespread behavior before the Neolithic, Keeley's (1996) new look at the archeological data suggests that recurrent raids could have seriously reduced some band populations, perhaps by 10% or more per raid. To the degree that such behavior prevailed during the later Paleolithic, further and serious amplification of group effects could have occurred. By combining data provided by Keeley (1996) with the more recent (tribal) findings of Soltis et al. (1995), rough estimates of prehistoric extinction rates could be attempted, but the data for foragers before the Neolithic are few.

We have seen that consensual decisions assist group selection in its competition with individual selection in two ways. The first is through homogenization of foraging strategies for individuals and families within the group, which assists the retention of altruistic traits because it vitiates the individual selection effects that work against them. The second is through a significant amplification of the phenotypic variation among nearby groups whenever they arrive at differing strategies of behavior, which assists the retention of altruistic traits because it intensifies the group effects that support them. I emphasize that this also intensifies the selective retention of *any* trait that is group beneficial, even if it is individually advantageous or selectively neutral rather than altruistic.

#### *Foragers Cope Actively with Free Riders*

So far, in combination egalitarian leveling and consensus seeking are serving to reduce phenotypic variation within groups while unanimous strategic decisions are amplifying phenotypic variation between groups. The net effect, for humans, is a major advance in the potential for traits that are generically altruistic to be selected. This means that free riding is less of a problem, yet in theory it is possible that even these augmented group effects could be offset by rampant selfish cheating. Again, human morality enters into the equation (see Boyd and Richerson 1992).

In setting their moral standards, foragers anticipate and try to resolve preemptively social problems that are directly relevant to reproductive success, defining them almost in those terms. Typical problems involve greed with respect to food, competition for breeding partners, aggression, and domination, and foragers are quite good at solving them by banding together to manipulate deviants. Social pressure may be led by individuals, but it is the threat or actuality of the entire group's mobilizing that forces more determined malefactors to mend their ways.

In human foraging bands, there is also a positive interest by group members in matters involving altruism or cooperation, which results in rules for sharing that also are morally enforced. Now let us turn to the famous free riders who have been of such interest to biocultural theorists. These social parasites, who use up resources critical to the health and survival of others, are of intense interest to foragers themselves (e.g., Lee 1979; Tanaka 1980; Altman and Peterson 1988; Petersen 1993). Because foragers cooperate as entire bands, merely identi-

flying slackers or cheaters to avoid them as partners (e.g., Frank 1994) will not necessarily work. This is because an ethic exists of always granting the requests of others within the band, while changing bands to avoid such people may involve more costs than benefits. However, such hunter-gatherers are sometimes in a position to resist demands to share (Draper 1975; Wiessner 1982), and this capacity obviously applies to outright slackers who try to take advantage of co-operating group members. Good-citizen types also have the social weapons to make such people feel very uncomfortable and place them under stress (e.g., Briggs 1970), but if really serious sanctions are invoked (e.g., Boehm 1993), they also have the power to damage their reproductive success very directly.

Mithen (1990) and Kelly (1995, p. 202) have emphasized the astute cost-benefit decisions that hunter-gatherers make about foraging or sharing, and I suggest that policing of cheaters is an effect of the same problem-solving capacity, by which long-term consequences of behavior are intuitively evaluated on an "actuarial" basis and coped with in a way that seems rational to foragers and scientists alike. In applying their great "political intelligence" (see Boehm 1997) to problems with free riders, foragers focus rather directly on major issues of reproductive success that preoccupy evolutionary biologists. When foragers suppress upstarts who would like to dominate their peers, they are thinking about food resources in addition to personal political autonomy; when they sanction cheaters (see Dugatkin 1992) or those who make too little effort, they are usually concerned with food procurement or distribution.

Our scientific free-rider theories arise from the assumption that antisocial opportunists can gain such substantial inclusive fitness advantages over vulnerable, generically altruistic, prosocially inclined individuals that altruistic traits will be driven to very low frequencies. However, humans deserve special consideration. We develop moral communities that go far beyond cheater detection, to engage in moralistic cheater manipulation that includes active punishment of cheaters (see Boyd and Richerson 1992). In terms of altruistic traits being selected, the empirical question is, How much damage can those with unusually strong opportunistic tendencies actually do to other group members who are disposed to cooperate but are also vigilant and manipulative?

In Briggs's (1970) very rich description of Inuit behavior, one sees that one Eskimo family, known for stinginess, is socially distanced by the rest of the band. This semipariah subgroup is obliged to camp on the other side of a small river, and food sharing by others is grudging. In one instance, a female free-loader from the pariah family is pressured very directly to contribute labor to the boiling of fish heads for everybody. However, she does so only once, and the low-level ostracism continues. Although this socially unattractive Eskimo woman might be gaining some small net profit from freeloading in the short term, over time this pattern of behavior distances her and her family from the rest of the band and jeopardizes their full participation in cooperation, which can become critical to survival when times become difficult. I emphasize that in normal times the strong hunter-gatherer ethic of never turning down a request to share gives such people an advantage of sorts; in hard times, however, the willingness of other group members to be taken advantage of may be reduced.

Another factor that is not mentioned in discussions of human free riders is that the partial tolerance exhibited toward nonaltruistic takers surely has to be geared to their being few in number. As shrewd cost accountants, foragers understand the losses involved, and one may be certain that as the number of would-be free riders in a band rises, the tolerance of the rest of the band for such behavior will be reduced. However, an important distinction must be made. The more productive band members are quite prepared to share with others who are less lucky or less skilled than they are or whose capacity to secure food has been impaired by injury, illness, or old age—problems that can befall any good citizen of the band. Such generosity prevails up to the point that it jeopardizes everybody's survival. For example, Eskimos may abandon old people who cannot walk when it is time to migrate, because they simply cannot support enough dogs to carry such people on sleds (Balikci 1970). By the same token, normally productive people can be expected to draw a sharp line with respect to others who do not make a serious effort to fend for themselves—and to do so precisely at the point that donations to free riders incur what they see as a significant burden.

A hypothetical example will clarify this matter of cutoff points. Say a lazy free rider is in our foraging group—not a blatant cheater but basically a lazy person who hunts rather seldom and always has some excuse. As one of the better hunters, I think about his behavior, and at the moment, because antelope are plentiful, I know that all he is costing me and my fellow hunters is potentially a little more time and effort hunting game and carrying meat. I concede him his share, for there are group rules about sharing and it is considered unseemly to deny a person in need—a basic rule that helps enforce cooperation among normally productive group members as ambivalent cooperators (see Blurton-Jones 1983; Peterson 1993). However, when game becomes scarce, I will perceive him quite differently: his lazy man's share will reduce my own small portion of meat, will contribute to my physical exhaustion, and will make me and my children hungrier and more prone to illness. As these reproductively relevant red flags are hoisted, my anger may join with the anger of others who work at hunting with a good will, to create a sense of group outrage. The next steps are denial of cooperation, sharp social disapproval, and possibly active sanctioning. Thus, the free-rider problem is largely neutralized in a very direct and focused manner, just when it matters the most reproductively.

In an important sense, the term *free rider* could be misleading in the analysis of gene selection, for some individuals covered by this term are lazy or devious freeloaders, whereas others are merely good citizens who are obliged to cash in on their "insurance programs." The first type of individual carries antisocial genes for free riding, and if successful he reduces the frequencies of altruistic genes. The second type of individual contributes willingly to group welfare (i.e., carries no free-rider genes) but because of circumstances beyond his control has to accept donations from others. To the extent that such circumstances affect all group members on a probability basis, these benefits average out, and frequencies of altruistic genes are not affected.

As a result, the legitimate unfortunates who are readily given significant free

rides—the unlucky, the injured, the ill, the aged—tend to carry only an average representation of free-rider genes. Cheaters who carry such genes and would exploit this altruistic system are treated quite differently from those whose needs are morally legitimate. Indeed, their theoretical genetic advantage is largely negated because aid is withheld when it is most reproductively valuable, and obviously their advantages could be wholly negated by the costs of having a generally bad social status. In a small band, in which social reputations and male hunting proficiency are well known, one's marriage prospects also can be affected by a free-riding approach to life.

Because the reproductive advantages of individuals inheriting free-riding traits tend to be suppressed and are suppressed increasingly as reproductive stakes rise, the potency of free-rider arguments against selection of altruistic traits is significantly reduced (see also Boyd and Richerson 1992 for a more technical analysis of allied problems). The result is a freer play for group selection effects to support generically altruistic traits that benefit beneficiaries who are truly needy and to support other types of cooperation as well.

#### EFFECTS ON THE NATURAL SELECTION BALANCE OF POWER

With three powerful cultural factors working in favor of selection at the level of groups larger than families, it is no longer so difficult to model the evolution of human cooperation or other altruistic behaviors of the generic variety. Overall, it seems quite unlikely that group effects actually approached parity with inclusive fitness effects. However, the long-term change in the balance of power would seem to have been substantial enough to permit selection of generically altruistic traits that involved significant group benefits, so long as the individual costs were not too high.

I offer this as a working hypothesis that seems plausible in the face of Campbell and Gatewood's (1994) mechanical requirements: the argument has been made chiefly in terms of variation at the level of phenotype. To be precise, cultural behaviors have modified phenotypic variation so as to change the fundamental balance of power between individual and group levels of selection. This places group effects in a position to operate quite strongly on collections of foragers who happen to be strategizing together at specific points in time, particularly when subsistence is threatened. Because we have been concentrating on selection of altruistic traits, I also have brought into the analysis cultural traditions of cheater detection and manipulation because as phenotypic behaviors they act so directly (and favorably) on the genetic retention of altruistic traits.

If we consider just the egalitarian syndrome's direct impact on phenotypic variation, I have argued that a substantial advantage accrued to group effects. I now address briefly the question of quantification for modeling the changes I have discussed. For humans, making precise estimates of variation at the level of phenotype would appear to be scientific *terra incognita*. However, to establish a standard for comparison, one might estimate the phenotypic variation for humans who live in small, hierarchical chiefdoms, using them as proxies for the

presumptively hierarchical, apelike predecessors of the egalitarian prehistoric foragers we have been discussing. One could then compare such estimates with estimates for extant foragers as proxies for prehistoric egalitarians. In effect, I have been doing this without any attempt at quantification in this preliminary treatment.

One can broaden the basis for comparison. For other hierarchical mammals, Ellis (1995) surveyed a large number of studies and concluded that alpha individuals do reap reproductive benefits from their status in a hierarchy. This would suggest that the presumably quite hierarchical hominid social organization that preceded prehistoric egalitarianism (see Knauff 1991) made for intense selection within the band.

The prehistoric transition to egalitarianism can be discussed briefly. Egalitarianism produces what amounts to a neutralized dominance hierarchy (see Boehm 1993) or, better, one that has had the direction of power reversed. I say this because a coalition of all the subordinates stays in firm control of group social life, deliberately heading off tendencies to form a male hierarchy. This development did not necessarily involve any major changes in the human genotype, for basic tendencies to dominate and submit and tendencies to form coalitions may have been all that was needed, along with a shared will to avoid domination and the political intelligence necessary to cooperatively head it off. An enhanced, language-based cultural capacity to elaborate and institutionalize such tendencies may not have been necessary, but it would have been very useful (see Boehm 1997).

Once power is firmly in the hands of undominated egalitarians who otherwise (most of them) would be subordinates, all that is needed is some way to transfer this cultural invention forward across generations. The moral community, working with a well-cognized and specifically communicated cultural tradition, would seem to have been the agency for transmission. On this basis, all three types of behavior discussed above were able to remain in place in a stable fashion, in spite of continuing alpha tendencies exhibited by the more able, aggressive, or fortunate individuals. Once such groups arise and develop the typical egalitarian syndromes that are found worldwide so long as foragers remain nomadic, selection between groups is in a position to compete much more strongly with selection that takes place within groups, and generically altruistic behavioral traits can be genetically supported.

Once this transition to leveled hierarchy, decision making by consensus, and moralistic manipulation of would-be free riders was in place as a basically phenotypic development, the new natural selection balance of power had many millennia to work on generically altruistic traits at the level of gene selection. The phenotypic transition could have come as late as with *Homo sapiens sapiens*, but it may well have been associated with large game hunting, which began earlier. The result was a mammalian species that remains distinctive in its propensity for cooperation and also all but unique in its capacity for imagining different behavioral blueprints or adaptive strategies and making them effective (Boehm 1978). It is this exercise of imaginativeness that makes likely the major



successes and blunders, crystallized in group decisions, that amplified phenotypic variation rates at the group level.

It is acknowledged universally that natural selection operates on phenotype, not on genotype. However, in the extended and otherwise thorough discussion of altruism and group selection, variation that is induced or reduced by cultural behaviors has been given little attention as a general factor that could be affecting selection mechanics. The reader must judge whether I have met Campbell and Gatewood's (1994) scientifically proper requirement that issues of selection mechanisms be addressed in their specifics, but I emphasize once more that I have been focusing squarely on the impact of patterned cultural behavior on phenotypic variation within and between groups. The conclusion is that so far as generically altruistic genes were concerned, group effects were significantly empowered in their struggle with inclusive fitness.

For other group-living mammals, there is some food for thought here. Wherever phenotypic variation at the individual level is suppressed for whatever reason, as with the subordinate coalitions of chimpanzees curbing the perqs of alpha males, selection of altruistic traits will be enhanced. Wherever groups make and enact reproductively significant decisions as groups and the decisions are prone to vary, group effects will be enhanced: Kummer's (1971) description of arid-country baboon (*Papio hamadryas*) migration decisions at the large-troop level provides an excellent example (see also Boehm 1978), and varying decisions of alpha-male leaders in species that stay constantly in large groups would also qualify. With respect to cheater detection, an extensive animal literature already exists.

Factors that may well be relevant for human foragers but that I set aside also may be relevant for other species. For example, in the case of East African chimpanzees (*Pan troglodytes schweinfurthii*), extinction rates are worth considering, with two severe group decimations already documented (Goodall 1979; Nishida 1979). The effect on selection mechanics may be quite complicated, however, as females are often changing groups whereas the males stay put. Vehrencamp's (1983) model might be of interest in this respect. Pleiotropic effects, mentioned in passing earlier, may well be supporting certain specific types of altruistic behavior, such as interventions in the quarrels of unrelated adults in species in which this is regularly practiced with respect to juvenile offspring (see Boehm 1981, 1994a). Any of these models would take some of the pressure off of inclusive fitness theory as an obviously powerful explanation that sometimes seems to be pushed to the point of contrivance.

#### GROUP SELECTION AND HUMAN NATURE

The argument has been about selection mechanics, specifically about selection mechanics as they become involved with selection of generically altruistic traits. For humans in particular, the reign of group selection as a significant player in the natural selection game prevailed for scores of millennia and surely for generations sufficient to produce major changes in the behavioral dis-

positions that make up our nature. This argument about cultural behavior impacting on selection mechanics can be made philosophical. Common sense tells us that human nature today involves a blend of selfishness, nepotism, and generically altruistic feelings and impulses and that certainly not all altruistic behavior is forced on selfish individuals by a moralistic society that places its interests above those of individuals. Far from it—anonymous donations to charities, for example, constitute persuasive evidence to the contrary. Much of current theory in social biology tells us, to the contrary, that the best we can do is to be selfish individuals who under many circumstances can turn into ardent nepotists and that when our altruism becomes generic, this behavior must be socially coerced.

The mechanical model I have provided here will allow for some serious rethinking of both the selection arguments of biologists and the philosophical positions of scholars in a variety of fields. I have proposed that while the human gene pool was being formed, group effects were substantially greater than most would acknowledge, whereas within-group/nepotistic effects were seriously damped. In this connection, it seems logical to assume that the division of labor between levels of selection should be directly reflected in human nature (see Campbell 1965; Nesse 1994). Within-group selection (with parental investment and kin selection) should make for selfishness and nepotism, whereas group selection should make for generic altruism, so long as this remains contained within the group. Human tendencies to ethnocentrism (see LeVine and Campbell 1972) assist in this containment.

On the basis of the above analysis, one can predict that human nature should contain some quite strong elements of generic altruism in addition to selfishness and nepotism. The generic traits are expressed through direct impulses and feelings that support giving assistance even to others with whom one is bonded socially but not genealogically. This is something we all experience, to varying degrees depending on our socialization and, in all probability, our individually varying genetic heritages too. It also is exemplified by the ideological attraction of humans to social ideologies that are altruistic—ideologies that range from hunter-gatherer codes of cooperation and helpfulness, to modern welfare-state ideologies, to the idealistic communist blueprints that have proven so very difficult to execute.

Human nature is structured to be ambivalent (Boehm 1989). At the same time that many people sincerely subscribe to these idealistic codes, they also routinely cheat on their income taxes and provide advantages wherever they can to their own offspring. Other people set aside their altruistic impulses to go with the other side of what is a basic ambivalence: they favor societal blueprints that openly or implicitly espouse individual selfishness. It is our ambivalent human nature that underlies these varying preferences and behaviors. My argument is that long ago, the genetic basis for this ambivalence was structured by the levels of selection that prevailed prehistorically, at a time when the egalitarian syndrome reigned universally and therefore cultural conditions were favorable to increased selection of generically altruistic traits.

## ACKNOWLEDGMENTS

M. Boehm, D. T. Campbell, J. Chisholm, B. Knauff, J. Lancaster, M. Muller, P. J. Richerson, G. Seaman, C. Stanford, G. Williams, D. S. Wilson, E. O. Wilson, and P. Wohlmuth have provided suggestions or useful criticisms.

## LITERATURE CITED

- Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–384.
- . 1987. The biology of moral systems. Aldine de Gruyter, New York.
- Alexander, R. D., and G. Borgia. 1978. Group selection, altruism and the levels of organization of life. *Annual Review of Ecology and Systematics* 9:449–475.
- Altman, J., and N. Peterson. 1988. Rights to game and rights to cash among contemporary Australian hunter-gatherers. Pages 75–94 in T. Ingold, D. Riches, and J. Woodburn, eds. *Hunters and gatherers*. Vol. 2. Property, power, and ideology. Berg, Oxford.
- Balikci, A. 1970. The Netsilik Eskimo. Waveland, Prospect Heights, Ill.
- Bennett, J. W. 1976. Anticipation, adaptation, and the concept of culture in anthropology. *Science* (Washington, D.C.) 192:847–853.
- Blurton-Jones, N. 1983. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology* 41:145–157.
- Boehm, C. 1976. Biological versus social evolution. *American Psychologist* 31:348–351.
- . 1978. Rational preselection from *Hamadryas* to *Homo sapiens*: the place of decisions in adaptive process. *American Anthropologist* 80:265–296.
- . 1981. Parasitic selection and group selection: a study of conflict interference in rhesus and Japanese macaque monkeys. Pages 160–182 in A. B. Chiarelli and R. S. Corruccini, eds. *Primate behavior and sociobiology*. Springer, Berlin.
- . 1982a. The evolutionary development of morality as an effect of dominance behavior and conflict interference. *Journal of Social and Biological Structures* 5:413–422.
- . 1982b. A fresh outlook on cultural selection. *American Anthropologist* 84:105–124.
- . 1984. Can hierarchy and egalitarianism both be ascribed to the same causal forces? *Politics and the Life Sciences* 1:34–37.
- . 1989. Ambivalence and compromise in human nature. *American Anthropologist* 91:921–939.
- . 1993. Egalitarian society and reverse dominance hierarchy. *Current Anthropology* 34:227–254.
- . 1994a. Pacifying interventions at Arnhem Zoo and Gombe. Pages 211–226 in R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne, eds. *Chimpanzee cultures*. Harvard University Press, Cambridge, Mass.
- . 1994b. Reply to Erdal and Whiten: “On Human Egalitarianism: An Evolutionary Product of Machiavellian Status Escalation?” *Current Anthropology* 35:178–180.
- . 1996. Emergency decisions, cultural selection mechanics, and group selection. *Current Anthropology* 37:763–793.
- . 1997. Egalitarian behavior and the evolution of political intelligence. In R. W. Byrne and A. Whiten, eds. *Machiavellian intelligence*. Vol. 2. Cambridge University Press, Cambridge (in press).
- Boyd, R., and P. J. Richerson. 1985. *Culture and evolutionary process*. University of Chicago Press, Chicago.
- . 1990. Group selection among alternative evolutionarily stable strategies. *Journal of Theoretical Biology* 145:331–342.
- . 1991. Culture and cooperation. Pages 27–48 in R. A. Hinde and J. Grobel, eds. *Cooperation and prosocial behavior*. Cambridge University Press, Cambridge.
- . 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171–195.

- Briggs, J. L. 1970. *Never in anger*. Harvard University Press, Cambridge, Mass.
- Campbell, D. T. 1965. Ethnocentric and other altruistic motives. *Nebraska Symposium on Motivation Papers* 13:283–311.
- . 1972. On the genetics of altruism and the counter-hedonic component of human culture. *Journal of Social Issues* 28:21–37.
- . 1975. On the conflicts between biological and social evolution and between psychology and moral tradition. *American Psychologist* 30:1103–1126.
- . 1983. The two distinct routes beyond kin selection to ultrasociality: implications for the humanities and social sciences. Pages 11–41 in D. Bridgeman, ed. *The nature of prosocial development interdisciplinary theories and strategies*. Academic Press, New York.
- . 1994. How individual and face-to-face-group selection undermine firm selection in organizational evolution. Pages 23–28 in J. A. C. Baum and J. V. Singh, eds. *Evolutionary dynamics of organizations*. Oxford University Press, New York.
- Campbell, D. T., and J. B. Gatewood. 1994. Ambivalently held group-optimizing predispositions: commentary on Wilson, D. S. and Eliot Sober, “Reintroducing Group Selection to the Human Behavioral Sciences.” *Behavior and Brain Sciences* 17:614.
- Cashdan, E. 1980. Egalitarianism among hunters and gatherers. *American Anthropologist* 82:116–120.
- . 1990. *Risk and uncertainty in tribal and peasant economies*. Westview, Boulder, Colo.
- Draper, P. 1975. !Kung women: contrasts in sexual egalitarianism in foraging and sedentary contexts. Pages 77–109 in R. Reiter, ed. *Toward an anthropology of women*. Monthly Review Press, New York.
- Dugatkin, L. A. 1992. The evolution of the con artist. *Ethology and Sociobiology* 13:3–18.
- Dunbar, R. 1996. *Grooming, gossip and the evolution of language*. Faber & Faber, London.
- Durham, W. H. 1976. Resource competition and human aggression. I. A review of primitive war. *Quarterly Review of Biology* 51:385–415.
- . 1991. *Coevolution: genes, culture, and human diversity*. Stanford University Press, Stanford, Calif.
- Edgerton, R. B. 1992. *Sick societies: challenging the myth of primitive harmony*. Free Press, New York.
- Eibl-Eibesfeldt, I. 1982. Warfare, man’s indoctrinability and group selection. *Zoologische Tierpsychologie* 60:177–198.
- . 1989. *Human ethology*. Aldine de Gruyter, New York.
- Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethology and Sociobiology* 16:257–333.
- Erdal, D., and A. Whiten. 1994. On human egalitarianism: an evolutionary product of Machiavellian status escalation? *Current Anthropology* 35:175–178.
- . 1996. Egalitarianism and Machiavellian intelligence in human evolution. Pages 139–150 in P. Mellars and K. Gibson, eds. *Modelling the early human mind*. McDonald Institute Monographs. McDonald Institute for Archeological Research, Cambridge.
- Frank, R. H. 1988. *Passions within reason: the strategic role of emotions*. Norton, New York.
- . 1994. Commentary on Wilson, D. S. and Eliot Sober, “Reintroducing Group Selection to the Human Behavioral Sciences.” *Behavior and Brain Sciences* 17:620–621.
- Fried, M. H. 1967. *The evolution of political society: an essay in political anthropology*. Random House, New York.
- Gardner, P. 1991. Foragers’ pursuit of individual autonomy. *Current Anthropology* 32:543–558.
- Goldschmidt, W. 1959. *Man’s way*. Holt, New York.
- . 1976. Biological versus social evolution. *American Psychologist* 31:355–356.
- Goodall, J. 1979. Life and death at Gombe. *National Geographic* 155:592–622.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. I, II. *Journal of Theoretical Biology* 7:1–16, 17–52.
- . 1991. Selection of selfish and altruistic behavior in some extreme models. Pages 57–92 in J. S. Eisenberg and W. S. Dillon, eds. *Man and beast: a comparative social behavior*. Smithsonian Institution Press, Washington, D.C.
- Heintz, H. 1972. Territoriality among the Bushmen in general and the !Ko in particular. *Anthropos* 67: 405–416.

- Hill, K. H. Kaplan, K. Hawkes, and A. M. Hurtado. 1987. Foraging decisions among Ache hunter-gatherers: new data and implications for optimal foraging theory. *Ethology and Sociobiology* 8:1–36.
- Keeley, L. H. 1996. *War before civilization: the myth of the peaceful savage*. Oxford University Press, New York.
- Kelly, R. L. 1995. The foraging spectrum: diversity in hunter-gatherer lifeways. Smithsonian Institution Press, Washington, D.C.
- Knauff, B. B. 1989. Sociality versus self-interest in human evolution. *Behavior and Brain Sciences* 12: 712–713.
- . 1991. Violence and sociality in human evolution. *Current Anthropology* 32:391–428.
- . 1994a. Culture and cooperation in human evolution. Pages 37–67 in L. Sponsel and T. Gregor, eds. *The anthropology of peace and nonviolence*. Rienner, Boulder, Colo.
- . 1994b. Reply to Erdal and Whiten. *Current Anthropology* 35:181–182.
- Kummer, H. 1971. *Primate societies: group techniques of ecological adaptation*. Aldine, Chicago.
- Laughlin, C. D., and I. A. Brady, eds. 1978. *Extinction and survival in human populations*. Columbia University Press, New York.
- Lee, R. B. 1976. !Kung spatial organization: an ecological and historical perspective. Pages 73–97 in R. B. Lee and I. DeVore, eds. *Kalahari hunter-gatherers: studies of the !Kung San and their neighbors*. Harvard University Press, Cambridge, Mass.
- . 1979. *The !Kung San: men, women, and work in a foraging society*. Cambridge University Press, Cambridge.
- . 1984. *The Dobe !Kung*. Holt, Rinehart & Winston, Chicago.
- LeVine, R. A., and D. T. Campbell. 1972. *Ethnocentrism: theories of conflict, ethnic attitudes, and group behavior*. Wiley, New York.
- Miller, G. F. 1994. Commentary on Wilson, D. S. and Eliot Sober, “Reintroducing Group Selection to the Human Behavioral Sciences.” *Behavior and Brain Sciences* 17:630–631.
- Mithen, S. J. 1990. *Thoughtful foragers: a study of prehistoric decision making*. Cambridge University Press, Cambridge.
- Moore, J. 1994. Commentary on Wilson, D. S. and Eliot Sober, “Reintroducing Group Selection to the Human Behavioral Sciences.” *Behavior and Brain Sciences* 17:614.
- Nesse, R. 1994. Commentary on Wilson, D. S. and Eliot Sober, “Reintroducing Group Selection to the Human Behavioral Sciences.” *Behavior and Brain Sciences* 17:633–634.
- Nishida, T. 1979. The social structure of chimpanzees of the Mahale Mountains. Pages 73–122 in D. A. Hamburg and E. R. McCown, eds. *The great apes*. Benjamin/Cummings, Menlo Park, Calif.
- Odum, E. P. 1993. *Ecology and our endangered life-support systems*. Sinauer, Sunderland, Mass.
- Palmer, C. T., B. E. Fredrickson, and C. F. Tilley. In press. Categories and gatherings: group selection and the mythology of cultural anthropology. *Ethology and Sociobiology*.
- Peterson, N. 1993. Demand sharing: reciprocity and the pressure for generosity among foragers. *American Anthropologist* 95:860–874.
- Price, T. D., and J. A. Brown, eds. 1985. *Prehistoric hunter-gatherers: the emergence of cultural complexity*. Academic Press, New York.
- Seeley, T. D. 1997. Honey bee colonies are group-level adaptive units. *American Naturalist* 150:S22–S41.
- Service, E. 1975. *Origin of the state and civilization: the process of cultural evolution*. Norton, New York.
- Simon, H. 1990. A mechanism for social selection and successful altruism. *Science* (Washington, D.C.) 250:1665–1668.
- Soltis, J., R. Boyd, and P. J. Richerson. 1995. Can group-functional behaviors evolve by cultural group selection? an empirical test. *Current Anthropology* 36:473–494.
- Strier, K. B. 1994. Brotherhoods among atelins: kinship, affiliation, and competition. *Behaviour* 130: 151–167.
- Tanaka, J. 1980. *The San hunter-gatherers of the Kalahari: a study in ecological anthropology*. University of Tokyo Press, Tokyo.

- Tiger, L., and R. Fox. 1971. *The imperial animal*. Delta, New York.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.
- . 1972. Parental investment and sexual selection. Pages 136–179 in B. G. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Aldine, Chicago.
- van Hoof, J. A. R. A. M., and C. P. van Schaik. 1992. Cooperation in competition: the ecology of primate bonds. Pages 357–390 in A. H. Harcourt and F. B. M. de Waal, eds. *Coalitions and alliances in humans and other animals*. Oxford University Press, Oxford.
- Vehrencamp, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* 31:667–682.
- Wade, M. J. 1978. A critical review of the models of group selection. *Quarterly Review of Biology* 53:101–114.
- Wiessner, P. 1982. Risk, reciprocity and social influences on !Kung San economics. Pages 61–84 in E. Leacock and R. B. Lee, eds. *Politics and history in band societies*. Cambridge University Press, Cambridge.
- Williams, G. C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, N.J.
- Wilson, D. S. 1975. A general theory of group selection. *Proceedings of the National Academy of Sciences of the USA* 72:143–146.
- . 1977. Structured demes and the evolution of group-advantageous traits. *American Naturalist* 111:157–185.
- . 1980. The natural selection of populations and communities. Cummings, Menlo Park, Calif.
- . 1983. The group selection controversy: history and current status. *Annual Review of Ecology and Systematics* 14:159–187.
- . 1989. Levels of selection: an alternative to individualism in biology and the social sciences. *Social Networks* 11:257–272.
- . 1990. Weak altruism, strong group selection. *Oikos* 59:135–140.
- . In press. Incorporating group selection into the adaptationist program: a case study involving human decision making. In J. Simpson and D. Kendrick, eds. *Evolutionary approaches in personality and social psychology*. Erlbaum, Mahwah, N.J.
- Wilson, D. S., and E. Sober. 1994. Reintroducing group selection to the human behavioral sciences. *Behavior and Brain Sciences* 17:585–654.
- Wilson, E. O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, Mass.
- . 1978. *On human nature*. Harvard University Press, Cambridge, Mass.
- Woodburn, J. 1982. Egalitarian societies. *Man* 17:431–451.